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INHERITANCE OF LENGTH OF POD IN CERTAIN CROSSES

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INTRODUCTION

The inheritance of a difference between two plants has sometimes, though not often, been studied both qualitatively and quantitatively. Correns (5)² has shown that this can be done even with differences in flower color. The inheritance of a large-size difference can occasionally be followed by mere inspection, as in crosses of some tall and dwarf races of peas (*Pisum sativum*) (13); sweet-peas (*Lathyrus odoratus*) (1, p. 280-281); beans (*Phaseolus vulgaris*) (8); and maize (*Zea mays*) (10).

Even with accurate measurements, however, it will probably not be possible to keep track of a single small-size difference, for its segregation may be masked by the modifications. But if several small genetic differences affect the size of the same plant organ, it would usually be still less possible to disentangle the segregation in the second generation of a cross, as Johannsen (12) has proved. The masking effect of the modifications may, however, be lessened by choosing those plant organs which are least liable to modification and which are also repeated many times on each plant, such as flowers (6) or pods with the modal number of consecutive ripe seeds (2). In one such case some of the members of a fraternity were grown on poles 8 feet apart, and others were sown at intervals of 4 feet in a thick row of sorghum. Though the crops of the stunted plants averaged only one-twentieth of those of the others, yet the average length of their 5-seeded pods reached 94 per cent of that of the pods of the well-nourished plants.

In the reciprocal crosses described in this paper, the length of pod was first studied qualitatively and then quantitatively. All the families

¹ I express my thanks to Messrs. C. D. Gunn and C. W. Long, of the Florida Experiment Station, for their careful work in measuring pods.

² Reference is made by number to "Literature cited," pp. 419-420.

grown were selected with the aim of obtaining useful agricultural plants. A fairly complete third generation was raised, but the fourth generation was the result of selection and was the opposite of a random sample.

QUALITATIVE INVESTIGATION

The Florida velvet bean (*Stizolobium deeringianum*) was crossed both ways with the Philippine Lyon bean (*S. niveum*). A pertinent description of these plants has been given in my account of the inheritance of semisterility (4). The Florida velvet bean has a short pod (Pl. XL, fig. B), while the pod of the Lyon bean (Pl. XL, fig. C) is about half as long again and is broader. The pods of the first-generation hybrid plants were as long as, or slightly longer than, those of the Lyon. The progeny of the hybrids in the second generation could be divided by inspection into short-podded plants and long-podded plants. The short pods could be identified, even when young, by their greater proportional width. Although both short pods and long pods varied greatly in size on different second-generation plants, yet no case was met with where the classification could not be carried out when all the pods on a plant were taken into account. Plate XL, figures A and D, shows typical pods of second-generation plants with pods shorter than the Florida velvet bean and longer than the Lyon bean pods. The difference between short and long pods was sharply marked in all the segregating third-generation families.

Tables I, II, and III give the results of field inspection, checked by examination of the pods after harvesting.

TABLE I.—Length of pods in first-generation bean crosses

Parentage. ^a	Number of plants with—	
	Long pods.	Short pods.
Florida velvet bean × Lyon bean.....	7
Lyon bean × Florida velvet bean.....	6
Total.....	13

^a The pollen parent is given last throughout this article.

TABLE II.—Length of pods in second-generation bean crosses

Parentage.	Progeny ratio.		Calculated ratio.		Deviation.	Probable deviation.
	Long.	Short.	Long.	Short.		
Florida velvet bean × Lyon bean.....	140	: 49	141.75	: 47.25	−1.75	4.0
Lyon bean × Florida velvet bean.....	375	: 120	371.25	: 123.75	+3.75	6.5
Total.....	515	: 169	513	: 171	+2.0	7.6

The most probable single ratios have been calculated on the hypothesis that there are three chances for the long pod to one chance for the short pod. However, by the theory of probability, a deviation from the whole numbers nearest to these calculated ratios is far more likely to occur than not. The most probable deviation has been calculated by the conventional formula,¹ and is given in the last column of Table II. Since the actual are not greater than the calculated deviations, it is probable that there is no interference with the random segregation of the long and the short pod, with three chances for the long to one chance for the short pod.

The third-generation families of the Florida velvet bean \times Lyon bean were grown in an elimination field among crowding sorghum, where there was some selective elimination of short-podded plants (3). Hence the ratios are useless here. Two long-podded parents, however, of those whose families were grown on poles gave a total of 49 long-podded to 13 short-podded (calculated, $46.5 \pm 2.3 : 15.5 \mp 2.3$). In the third generation of the Lyon bean \times Florida velvet bean, 17 families of more than 8 members each from long-podded parents were grown on poles. The totals of the 11 segregating families among these amounted to 231 long-podded and 76 short-podded plants, the calculated nearest whole numbers being 230 and 77. The long-podded homozygotes could not be distinguished by inspection from the heterozygotes. These results are given in Table III. The abbreviations used in this and the subsequent tables in this paper are "V" for Florida velvet bean and "L" for the Lyon bean.

TABLE III.—Length of pods in third-generation bean crosses from long-podded parents

Parentage.	Progeny ratio.		Calculated ratio.		Deviation.	Probable deviation.
	Long.	Short.	Long.	Short.		
LV-92.....	23	: 0
LV-548.....	30	: 0
LV-569.....	38	: 0
LV-558.....	20	: 0
LV-27.....	28	: 0
LV-311.....	9	: 0
LV-80.....	25	: 12	27.75	: 9.25	-2.75	± 1.8
LV-113.....	22	: 6	21	: 7	+1.0	± 1.5
LV-279.....	24	: 6	22.5	: 7.5	+1.5	± 1.6
LV-486.....	31	: 7	28.5	: 9.5	+2.5	± 1.8
LV-91.....	21	: 4	18.75	: 6.25	+2.25	± 1.5
LV-114.....	13	: 4	12.75	: 4.25	+0.25	± 1.2
LV-310.....	26	: 8	25.5	: 8.5	+0.5	± 1.7
LV-468.....	15	: 10	18.75	: 6.25	-3.75	± 1.5
LV-527.....	15	: 8	17.25	: 5.75	-2.25	± 1.4
LV-461.....	28	: 8	27	: 9	+1.0	± 1.8
LV-392.....	11	: 3	10.5	: 3.5	+0.5	± 1.1
Total.....	231	: 76	230.25	: 76.75	+0.75	± 5.1

¹ I have used the ordinary formula for probable deviation, which, however, does not seem to be appropriate (except with large numbers) to any but a 1 to 1 segregation. East and Hayes's practical test of this formula with large numbers (7) shows that it will in that case fit a 3 to 1 segregation with sufficient accuracy. Hence, the calculated probable deviations in Table III, where the numbers are small, are not reliable.

Out of these 11 segregating families, 5 show proportions with a greater deviation than the probable and 6 have a less deviation. The chances for deviations above and below the probable are theoretically equal. The greatest deviation is less than three times the probable. In 3 of the families the calculated numbers occur, since fractions of plants are impossible. Of the other families 5 show an excess of long-podded and 3 an excess of short-podded plants. Hence, the ratios for the third generation conform closely to the theory of probability. However, a further test can be made. It seems that a perfectly random distribution, with three chances for long pods to one chance for short pods, should give for any number of equal groups of n plants each a frequency distribution of numbers of long-podded plants in the groups in classes from n to 0 which corresponds to the terms of the binomial $(3 + 1)^n$. If all the segregating families of the third generation are divided into 76 consecutive groups of 4 plants each in the same order as grown in the field, omitting the last 3 plants out of the total of 307, we have the groups as given in Table IV.

TABLE IV.—Third-generation segregating families in groups of four plants

Pods.		Groups.		Deviations.
		Found.	Calculated.	
<i>Long.</i>	<i>Short.</i>			
4	: 0	27	24	+3
3	: 1	27	32	-5
2	: 2	18	16	+2
1	: 3	4	4	0
0	: 4	0	0	0

There is, thus, a fair agreement of the actual figures with those calculated for a random distribution with three chances for long to one chance for short pods.

Of the random sample of 17 families from long-podded parents given in Table III, 11 families segregated into long podded and short podded, while 6 families were constantly long podded. The calculated nearest whole numbers are also 11 and 6.

Eleven second-generation short-podded plants gave only short-podded progeny. One of these has been grown to the fifth generation, giving only short-podded progeny. Four second-generation long-podded plants which were constant in the third generation have been grown to the sixth generation on a field scale without throwing any short-podded progeny.

Therefore, the whole of the second-generation plants were probably in the proportion of 1 constant short-podded to 1 constant long-podded to 2 heterozygous long-podded plants.

Now, we must assume, with Mendel, Correns, and Bateson, that this difference of long-podded and short-podded plants corresponds to a difference between the pollen grains and egg cells of the Florida velvet

bean, on the one hand, and those of the Lyon bean, on the other. But, according to the special investigations of Strasburger and his coworkers, only a sperm nucleus without cytoplasm passes from the pollen tube to the egg cell in most angiosperms. If this is the case here, the progeny of the Florida velvet bean \times Lyon bean receives cytoplasm only from the Florida parent; and the progeny of the reciprocal cross has cytoplasm only from the Lyon bean. Hence, the genetic difference which determines the visible difference between long and short pods is a difference of the nuclei, not a difference of the cytoplasm. If we call this particular nuclear difference of the gametes, $E-e$, the nuclear difference of the zygotes (the Florida velvet bean and the Lyon bean plants) will be E_2-e_2 . ($E_2=E+e$.) Since we have no definite base of measurement, it is useful in many cases to take the recessive as our base and to regard e as zero. This is merely a convention.

To sum up, the Florida velvet bean and the Lyon bean have one main genetic difference affecting pod length. This genetic difference segregates in typical Mendelian fashion.

QUANTITATIVE INVESTIGATION

Investigators of the inheritance of differences in size have found that in many cases these differences are inherited as if several genetic differences (factors) were concerned and dominance was lacking. For instance, in East's masterly investigation of the inheritance of flower size in crosses of two species of *Nicotiana* (6), the first-generation mean flower length was near the geometrical mean of the parent flower lengths, while the second-generation mean was only slightly greater. The frequency array of the flower lengths of the second-generation plants formed a continuous series between the two grandparental means, with the mode below the center. If dominance had been present, the second-generation mean would have been less than the first-generation mean and the first-generation mean should have approached that of the long-flowered parent (supposing all factors were positive). Emerson (9) obtained similar results from a cross of short and long squashes (*Cucurbita pepo*). Groth (11) in many crosses of tomato (*Lycopersicon esculentum*) found the first-generation fruit length near the geometrical mean of the parent lengths. However, the strict proof of this absence of dominance demands, I think, the isolation of a family in which only one such genetic difference is segregating.

The hypothesis that size factors act as multipliers was, I believe, first applied by East (6). Groth's results are readily explicable on this hypothesis. A similar assumption has been made by Punnett and Bailey (14).

To sum up, previous work favors the hypothesis that some size factors show no dominance and act as multipliers.

PARENT PLANTS

In 1910 the mean of the averages of all the ripe 5-seeded pods on 11 plants of the Florida velvet bean (pedigreed line) was 62.9 mm. The mean of the average lengths of the 5-seeded pods of 9 plants of the Lyon bean (pedigreed line) was 92.7 mm. Some of these Lyon bean plants grew in a sandy spot and were stunted; hence the calculated mean is probably too low.

In 1912 the mean of the averages of all the 5-seeded pods of 2 pedigreed Florida velvet bean plants was 62.8 mm. and that of 2 pedigreed Lyon bean plants was 94.5 mm. These plants were grown on poles and were kept free from caterpillars. From 4 more Florida velvet bean and 42 more Lyon bean plants, of the same families, large samples were picked, and all the 5-seeded pods in these samples were measured, but in picking such samples the conspicuous best racemes are probably picked first, and the averages (63.2 and 95.6), which include these samples, are probably too high.

To sum up, the most reliable measurement of the average length of the dry 5-seeded pods of the pedigreed line of the Florida velvet bean was probably 62.8 mm. and that of the Lyon bean 94.5 mm.

FIRST GENERATION

The 5-seeded pods of the 7 first-generation plants were not separately measured in 1909, although many pods were measured. The measurements of 883 seeds from all parts of the pod gave an average of 15.5 mm. The measurements of 613 seeds of the Lyon bean from all parts of the pod gave an average of 15.1 mm. The excess of the first-generation seed length over that of the Lyon bean is in part, or wholly, due to the many gaps in the seed rows of the semisterile first-generation plants. These gaps permit the rounding off of the ends of the seeds, whereas the Lyon bean seeds are usually flattened at the ends by mutual pressure. For five seeds, the maximum excess of the hybrids over the Lyon bean thus is 2 mm.

In 1911 the six first-generation plants were more or less frosted. Only three 5-seeded pods were measured, averaging 98 mm.

To sum up, the average length of the 5-seeded pods of the first-generation plants is probably less than 2 mm. above that of the Lyon bean.

SECOND GENERATION

In Table V are given the frequency arrays of the average lengths of the ripe 5-seeded pods of the plants with white shoots of the second generations of the reciprocal crosses. The plants with black shoots (three-sixteenths of the whole) are not included, because they usually either bore no pods or bore few pods on large plants and so had their pod length physiologically increased. A trial showed that when all

young pods except eight were removed from a plant of the Florida velvet bean the length of 5-seeded pods increased from 63 to 73 mm. The plants in 1912 were grown in an especially favorable season, and more of the late plants had time to ripen their pods than in 1910.

TABLE V.—Frequency arrays of the average lengths of ripe 5-seeded pods of bean plants with white shoots of second generations of the reciprocal crosses (classes of 3 mm.)

FLORIDA VELVET BEAN X LYON BEAN, 1910																								
Length of pod, mm.	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100	103	106	109	112	115	Average lengths.	Total number of plants.
Florida velvet bean				6	4	1								1	5	2	1						Mm.	
Lyon bean																X							62.9	11
F ₁ hybrids																							92.7	9
F ₂ hybrids	1	4	8	10	9	8	4	1	1		8	17	9	23	25	11	13	10	7	4	2		62.7 and 94.2	46 and 129
F ₂ parents		(1)	(1)								(1)	(2)	(1)	(2)	(3)	(2)	(2)	(6)	(2)	(1)	2(1)			

LYON BEAN X FLORIDA VELVET BEAN, 1912																								
Length of pod, mm.	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100	103	106	109	112	115	Average lengths.	Total number of plants.
Lyon bean														1	22	16	5						95.6 (94.5)	44
Florida velvet bean				1	5																		62.2 (62.8)	6
F ₁ hybrids																X							98.7	
F ₂ hybrids	1	12	16	20	24	12	9	5	1	2	11	21	38	49	60	51	24	33	13	10	3		62.7 and 94.7	100 and 315
F ₂ parents											(1)		(1)	(2)	(2)	(2)	2(1)	(4)						

^a Black plant.

The actual averages ¹ were:

	Short pods.	Long pods.
1910.....	62.7	94.2
1912.....	62.7	94.7

These are sensibly the same as the most trustworthy averages (62.8 and 94.5 mm.) for the Florida velvet bean and the Lyon bean in 1912. The average of the first-generation plants is probably near 95 mm. The average of the long-podded plants of the second generation is 94.7 mm. Therefore, the factor *E* is probably completely dominant.

Thus, in the second generation the short pods and the long pods give the grandparental averages. The minor factors affecting pod length have not perceptibly altered the averages by their segregation, which agrees with the conclusion that *E* was completely dominant and the minor factors showed zero dominance and acted symmetrically with regard to both long and short pod, decreasing and increasing to the same extent each parental pod length. Calculation shows in this case that the increase of the second-generation averages over the parental lengths, which is a consequence of the hypothesis that the factors act as multipliers, is so small as to be negligible.

¹ The averages have been calculated from the actual figures, not from the frequency classes.

Dividing the second-generation variates into groups on each side of the means, we have:

Year.	Number of short pods.		Number of long pods.		Differences.
	Below mean.	Above mean.	Below mean.	Above mean.	
1910.....	24	22	71	58	2 and 13
1912.....	51	49	165	150	2 and 13 2 and 15

In each case there are fewer variates above than below the mean. This agrees with the hypothesis that the factors act as multipliers.

The second-generation means, including both short and long, were 85.9 and 86.9 mm. These two determinations average 86.4 mm. If E is completely dominant and the minor factors act symmetrically, the second-generation mean will be $\frac{1}{4}(62.8 + 3 \times 94.5) = 86.6$. This is sensibly the same as the actual average, 86.4.

If factor E is a multiplier and completely dominant, we may find its multiplying value in several ways:

Parents—

1910..Lyon bean+Florida velvet bean= $92.7+62.9=1.47$. (Lyon bean value is too low.)

1912..Lyon bean+Florida velvet bean= $94.5+62.8=1.50$. (Two plants each.)

1912..Lyon bean+Florida velvet bean= $95.6+63.2=1.51$. (Including samples.)

Second generation—

1910..Long+short= $94.2+62.7=1.50$.

1912..Long+short= $94.7+62.7=1.51$.

This gives 1.50 to 1.51 for the multiplying value of Ee or E_2 compared with e_2 .

The extremes of the two crosses were:

	Short pods.	Long pods.
1910.....	52 and 76	81 and 113
1912.....	53 and 75	79 and 113

The results in the third and fourth generations show that these extreme values are inherited. The values of 1912 are probably the more reliable. If E is completely dominant and the factors are multipliers, the multiplying value of E is given by:

Shortest long pod+shortest short pod= $79+53=1.49$

Longest long pod+longest short pod= $113+75=1.51$

If E had shown incomplete dominance, the second value should have been markedly greater than the first. The average multiplying value of Ee or E_2 is here 1.50.

The square root of the product of the extremes should give the means nearly and the grandparental means more nearly.

$$\begin{array}{lll} \sqrt{53 \times 75} = 63.0 & \text{Mean} = 62.7 & \text{Grandparental mean} = 62.8 \\ \sqrt{79 \times 113} = 94.5 & \text{Mean} = 94.7 & \text{Grandparental mean} = 94.5 \end{array}$$

Lastly the combined multiplying value of all the minor factors (when double) is given thus:

Quotient of extremes of short-podded plants.....	75 ÷ 53 = 1.42
Quotient of extremes of long-podded plants.....	113 ÷ 79 = 1.43

The standard deviation in the second generation was:

	Short pods.	Long pods.
1910.....	5.1	7.4
1912.....	5.2	6.8

That the standard deviation of the long-podded is greater than that of the short-podded plants is in agreement with the hypothesis that the minor factors act as multipliers. If E is completely dominant, there is no difference in the action of Ee and E_2 to increase the standard deviation of the long-podded plants. The ratios of the two standard deviations in each of the two crosses (1.4 and 1.3) are not quite 1.5, as theory would seem to demand if all the variation were genetic. (See, however, below.)

The coefficients of variation were:

	Short pods.	Long pods.
1910.....	8.2	7.8
1912.....	8.3	7.2

If the variation were purely genetic, these coefficients should, I think, be nearly equal. East (6), however, gives the variation coefficient of the corolla-tube lengths of two parent lines of *Nicotiana* spp. as 8.9 for the short-flowered (170) plants and 6.8 for the long-flowered (167) plants. This variation was presumably not genetic. Judging from this, any modifications would tend to increase the coefficient of variation of the short-podded more than that of the long-podded plants. Hence, it is possible that the slight lowering of the standard deviation of the long-podded plants from the theoretical 1.5 to 1.4, or 1.3 times that of the short-podded plants, is an effect of modifications. Hence, this result does not, I think, disagree with the hypothesis that the factors act as multipliers.

That neither short-podded nor long-podded second-generation plants show a significant increase in either range or standard deviation by more than doubling their number seems to indicate that the genetic series can be fully developed with about 50 plants. But the absence of linkage has not been proved, and until this has been done no definite deductions as to the number of minor factors can be made.

The ranges are:

	Short pods. Mm.	Long pods. Mm.	Ratio of long to short pods.
1910.....	24	32	1.33
1912.....	22	34	1.55

On the hypothesis of factors acting as multipliers, the range of the long-podded plants should be about 1.5 times that of the short-podded plants, as it is in the more reliable 1912 results.

To sum up, the results of investigation of the second generations agree with the hypotheses that all the factors act as multipliers; that factor E is completely dominant; that the minor factors show zero dominance; that the minor factors act symmetrically with regard to each of the two grandparental lengths, which is not the case in a cross of the Florida velvet bean by the Yokohama bean (*Stizolobium hassjoo*).

THIRD GENERATION

Table VI gives all the third-generation families, grown in the elimination field, which segregated measurable short podded; and also all which did not, but had eight or more measurable survivors. Because of the crowding, these results are not so reliable as those given in Table VII, which include all the families grown on poles in 1913.

TABLE VI.—Frequency arrays of the average lengths of ripe pods of the third generation Florida velvet bean \times Lyon bean (classes of 3 mm.)

[The asterisk (*) shows the pod length of the parent plant of the family.]

Parentage.	Progeny.																								Average length of pod.	
Length of pod, mm.	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100	103	106	109	112	115	118	121	Mm.
VL-292	1	1								1	1			3	3	3	3	1								84
VL-133	1													2	3	3	3	3								88
VL-171	1													1	1	1	1	3	*							91
VL-325					1									1		1	1	1								92
VL-88					1	1	1	2	1					1	1	3	1	1	1	*						93
VL-509					1	1	1	2	1					1	1	3	1	1	1		2	1	1	1		94
VL-164					1	1	1			1				1	1	3	1	1	1		2	1	1	1		95
VL-294																		2	3	6	4	4	1	1	1	96
VL-85										1	1				1	1	1	1	1	*	3	3	2	2		97
VL-158	1	2	3		*	4																				98
VL-569																										99
VL-319						2	*	2	3	1	2			1	1	*	2	3								100
VL-147														1	1	2	3									101
VL-114														1	1	2	3	*	1							102
VL-255														1	1	1	1	1	1	*						103
VL-92														1	1	1	1	1	1							104
VL-94														1	1	1	1	1	1	*						105
VL-194														2	1	1	2	2	1		1	3				106
VL-610														1	1	*	1	1	3		3	1				107
VL-102														2	3	3	1	1	1		1	2	2			108
VL-120														1	1	1	1	1	1		1	1	1	1		109
VL-177														1	1	1	1	1	1		1	1	1	1		110
VL-251														1	1	1	1	1	1		1	1	1	1		111
VL-515 ^b														1	1	1	1	1	1		1	1	1	1		112
VL-297 ^b														1	1	1	1	1	1		1	1	1	1		113
VL-480																	1	3	2	3		*	2			114
VL-515 ^c																	1	1	3	5	5	5	2	1		115
VL-297 ^c																		2	1	1	1	*	2			116

^a The averages for the first nine families refer to the long-podded plants alone.

^b Grown in the elimination field in 1911.

^c Grown on poles in 1912.

TABLE VII.—Frequency arrays of the average length of ripe pods of the third-generation Lyon bean \times Florida velvet bean (classes of 3 mm.)

(The asterisk (*) indicates the pod length of the parent of the family)

F ₂ parentage.	F ₂ progeny.																								Average length of pod.
Length of pod.....mm.	49	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100	103	106	109	112	115		
LV-113.....	3	1		1							5	5	3		4										Mm. 80
LV-297.....											5	3	6		2	*	1		1						81
LV-468.....		1	1	3								4			1	1	3	3							90
LV-461.....												2	7	4	1	8	2	1		1					90
LV-319.....															3	3	3	2	2	1	1				95
LV-480.....																*	2	3	1	1	1	1			96
LV-522.....				3	3	1	1								1		3	1	2	1	1	1			96
LV-468.....				1	1	3	2					2	1		5	6	5	5	1	2	1				96
LV-114.....															1		2	2	1	1	1				99
LV-91.....																1	2	2	1	6		1	1		101
LV-92.....														1	3	1	5	3	1						92
LV-538.....														1	2	4	4	4	1	1	1				95
LV-27.....														1	1	2	5	5	5			1			98
LV-548.....															1	2	3	3	3	5	1			1	99
LV-299.....																3	4	3	4	2	3	2			99

In length of pods, VL-319 and LV-113 are the two lowest families from long-podded parents. The family of VL-319 ranges from 76 to 88 mm. and seems homozygous for *E*; that of LV-113 ranges from 76 to 85 mm., and throws short-podded, ranging from 49 to 58 mm. The parental lengths were 82 and 79 mm., respectively. To all appearances these two families are homozygous recessives for minor factors (regarded as positive).

VL-480 and VL-85 are the two highest families with the highest averages. (VL-297 was a nearly normal black plant throwing velvet.) The family of VL-480 ranges from 97 to 112 mm. and is homozygous for *E*. VL-85 ranges from 88 or 94 to 112 and throws short-podded of 70 to 73 mm. long. The parental lengths were 113 and 106 mm., respectively. VL-480, as shown in the fourth generation, is apparently homozygous for all minor factors, as well as for *E*.

Thus, both near the minimum and near the maximum of the second-generation long-podded plants, we find plants homozygous and heterozygous for *E*. Hence, *E* is probably completely dominant.

The numbers in each family are not large enough to determine the separate ranges. The fifth and last lines of Table V show the pod lengths of the parents of these families. The correlation between the average pod lengths of the long-podded parents and the averages of the long-podded plants of their progenies is 82 ± 5 per cent for 36 third-generation families.

The range of the short-podded plants in the various families is from 49 or 52 to 73 mm., and that of the long-podded from 73 to 118 mm. in the elimination field (omitting the black plant, VL-297) and from 76 to 115

mm. for the plants grown on poles. These ranges do not seem to differ significantly from the second-generation ranges.

The families are arranged according to the means of their long-podded plants. LV-310, exceptionally, as was marked in the field, throws short-podded plants with pods unusually long in comparison with those of its long-podded progeny. Whether this is a genuine exception can only be determined by growing further generations from it. This is being done.

In Table VIII the averages of the short-podded plants in each family are compared with the averages of the long-podded plants in the same families. If *E* is completely dominant and none of the minor factors show linkage (coupling or repulsion) with *E*, then the average ratio of the pod length of long-podded to short-podded plants should be about 1.5 in each family. With the exception of the family of LV-310, the ratio comes as close to 1.5 as can be expected in small families, averaging 1.52.

TABLE VIII.—Comparison of the length of pods of the short-podded plants in each family with those of the long-podded plants in the same families. Third generation. Parents heterozygous for *E*

Parentage.	Pod length of parent.	Pod length of progeny.		Ratio of lengths.	Difference from parent.
		Average of short-podded plants.	Average of long-podded plants.		
	<i>Mm.</i>	<i>Mm.</i>	<i>Mm.</i>		
LV-113.....	79	51.2	80.3	1.57	+ 1
LV-279.....	88	57.3	81.1	1.42	- 7
VL-292.....	88	53.0	83.8	1.58	- 4
VL-133.....	86	60.2	87.8	1.46	+ 2
LV-461.....	94	56.0	89.6	1.60	- 6
LV-468.....	92	58.4	89.7	1.54	- 2
VL-171.....	101	59.8	90.5	1.51	-10
VL-88.....	103	65.8	93.3	1.42	-10
LV-310.....	95	71.0	95.4	1.34	0
LV-80.....	91	60.3	95.5	1.58	- 5
LV-486.....	100	61.1	96.2	1.58	- 4
LV-527.....	95	62.6	96.4	1.54	+ 1
LV-114.....	98	62.5	99.3	1.59	+ 1
VL-509 a.....	93	65.8	101.6	1.55	+ 9
VL-104.....	98	65.0	102.7	1.58	+ 5
VL-85.....	106	71.0	103.5	1.46	- 2
Average.....				1.52	- 2

a Part of this family was grown on poles.

If the minor factors show zero dominance, the average of the long-podded progeny in each family should equal the parental average, the theoretical excess here being negligible. On the whole, the long-podded plants average 2 mm. shorter than their parents. This is in part due to the stunting in the elimination field, and also possibly to the severe drought in 1913. In both cases the third-generation families were

grown under more adverse conditions than were their second-generation parents.

Table IX compares the parental and progeny pod lengths of families not known to throw short-podded. The averages of the progenies are here less than the parental averages by 3.5 mm. (See above.)

TABLE IX.—Comparison of the pod length of the parents and progeny of families not known to throw short-podded. Third generation. Parents probably or certainly homozygous for *E*

Parentage.	Pod length of parent.	Average pod length of progeny.	Difference from parent.	Parentage.	Pod length of parent.	Average pod length of progeny.	Difference from parent.
	<i>Mm.</i>	<i>Mm.</i>			<i>Mm.</i>	<i>Mm.</i>	
VL-570 ^a	82	83	+1	VL-102.....	102	99	- 3
VL-147 ^a	85	86	+1	VL-194.....	103	99	- 4
VL-114.....	93	89	-4	LV-569.....	104	99	- 5
VL-255.....	97	90	-7	VL-120 ^a	101	100	- 1
VL-92 ^a	92	92	0	VL-177 ^a	105	101	- 4
LV-92.....	96	92	-4	VL-251.....	108	101	- 7
LV-558.....	94	95	+1	VL-515.....	104	102 (109)	- 2 (+5)
VL-94 ^a	104	97	-7	VL-297 ^b	115	102 (110)	-13 (-5)
LV-27.....	103	98	-5	VL-480.....	113	105	- 8
VL-610.....	95	99	+4				
LV-548.....	102	99	-3	Average.....			- 3.5

^a F₂ plants not certainly known to be homozygous for *E*.

^b A black plant throwing velvet.

To sum up, investigation of the third generation gives evidence that *E* is completely dominant; that its multiplying value is 1.5 (one family being an exception); that the genetic range of pod length was fully developed in the second generation; that the minor factors show zero dominance.

FOURTH GENERATION

The frequency arrays of fourth-generation families are given in Table X. By this time it was, of course, known which second-generation plants were *Ee*, and only two *Ee* families were grown. It was not possible to select directly for long-podded plants homozygous for *E*, as selection could only be made after growing the progeny. If the minor factors show zero dominance, selection for specially long pods should be speedily efficacious. Among other desirable characters, extra length of pod was sought for. Hence, the chances were that most selected third-generation plants would be the homozygotes in their families with regard to minor factors.

TABLE X.—Frequency arrays of the average length of ripe pods of fourth-generation crosses of beans (classes of 3 mm.)

[The asterisk (*) shows the parental pod length]

F ₂ parentage.	F ₁ progeny.																								Average length of pod.	
Length of pod...mm.	52	55	58	61	64	67	70	73	76	79	82	85	88	91	94	97	100	103	106	109	112	115	118	121		
VL-10-1.....	1	4	2	*1	2																				Mm.	
LV-486-36.....	1	3		*3																						59
LV-486-35.....	3	1											2	5	*1	2	1									56 and 59
LV-92-2.....													*	3	1	3										91
LV-92-6.....													1	*11	8	1										91
LV-92-35.....													4	4	1											89
LV-92-40.....													2	0	3		*									88
VL-216-1.....													3	3	9	9	*1	1								91
LV-558-17.....													*	2	7	0	3									91
LV-558-24.....													2	3	3	3	3									91
LV-558-13.....													1	1	1	1										91
LV-558-9.....													3	3	*2	1										91
LV-558-11.....													2	3	3	*1										94
LV-569-22.....														5	3	1										92
LV-569-40.....														1	3	3										95
LV-569-6.....														4	2		*									92
LV-569-23.....														1	3	2		*5								96
LV-91-16.....														2	3	4		*0	0	1						99
LV-91-4.....																	4	0	*3	4						102
VL-85-15.....																	2	0	3	*3	2					57 and 104
VL-480-6.....																										107
VL-515-21.....																	*	4	*15	3	3	2				105
VL-515-22.....																	1	*1	12	15	0	0	1			101
VL-515-23.....																	3	0	10	8	2					106
VL-515-35.....																	3	*2	0	13	5	0	1			108
VL-515-1.....																	3	1	0	1	3	2				108
VL-515-27.....																	2	*5	2	0	0	1				109
VL-515-31.....																	2	4	9	10	1	1				107
VL-297-23.....																	*	2	1	5	1					109
VL-297-19.....																	*2	4	8	10	4	2	1			109
VL-297-5.....																		2	*6	11	5	1				109
VL-297-11.....																	1	0	0	7	2	1	*			109

One family (from *Ee* parent), LV-486-35, shows a ratio of long-podded mean to short-podded mean of 1.5.

In the families of LV-92, the parents ranged from 82 to 97. The progenies did not sensibly differ. Judging by these, LV-92 was homozygous for minor factors. The same applies to the families of VL-297.

On the other hand, the families of VL-515 showed evidence of the segregation of a minor factor; a segregation also marked in the field.

No indubitable evidence of segregation can be seen in the other fourth-generation families.

In Table XI the pod lengths of the third-generation parents are compared with those of their long-podded progenies. The average of the whole shows an insignificant excess of pod length in the progenies.

TABLE XI.—Comparison of the pod lengths of third-generation parents with those of their long-podded progeny

Parentage.	Pod length of parent.	Average pod length of progeny (long-podded).	Difference from parent.	Parentage.	Pod length of parent.	Average pod length of progeny (long-podded).	Difference from parent.
	<i>Mm.</i>	<i>Mm.</i>			<i>Mm.</i>	<i>Mm.</i>	
LV-486-35...	92	89	- 3	LV-91-16...	104	99	- 5
LV-92-2...	81	91	+10	VL-85-15...	105	104	- 1
LV-92-6...	87	89	+ 2	VL-480-6...	105	107	+ 2
LV-92-35...	93	87	- 6	VL-515-21...	98	105	+ 7
LV-92-40...	90	88	- 2	VL-515-22...	99	105	+ 6
VL-216-1...	96	91	- 5	VL-515-23...	101	106	+ 5
LV-558-17...	87	93	+ 6	VL-515-35...	103	108	+ 5
LV-558-24...	94	93	- 1	VL-515-1...	105	108	+ 3
LV-558-9...	94	93	- 1	VL-515-27...	105	109	+ 4
LV-558-13...	95	92	- 3	VL-515-31...	108	107	- 1
LV-558-11...	98	94	- 4	VL-297-23...	98	109	+11
LV-569-22...	93	92	- 1	VL-297-19...	99	109	+10
LV-569-40...	93	95	+ 2	VL-297-5...	107	109	+ 2
LV-569-6...	96	92	- 4	VL-297-11...	121	109	-12
LV-569-23...	100	96	- 4				
LV-91-4...	102	102	0	Average			+0.5

To sum up, the fourth-generation families show either that selection for long pod had been effective in isolating plants homozygous for minor factors or that segregation of the residual minor factors was in most cases masked by the modifications.

SUMMARY

(1) A single genetic difference, E , is responsible for the main difference between short and long pods. This genetic difference segregates in normal Mendelian fashion.

(2) Factor E is completely quantitatively dominant, so that $E_2 = Ee$.

(3) This factor acts as a multiplier, with a multiplying value of about 1.51.

(4) Minor factors for pod length also act as multipliers, with a combined multiplying value (when double) of about 1.42.

(5) These minor factors apparently show zero dominance, in the sense that if $A_2 B_2 C_2 \dots$ are positive double factors with a combined multiplying value of x , the value of $AaBbCc \dots$ is \sqrt{x} .

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PLATE XL

Typical 5-seeded bean pods, showing the length of parents and crosses; *A*, One of the shortest second-generation pods; *B*, the Florida velvet-bean pod; *C*, the Lyon-bean pod; *D*, one of the longest second-generation pods.



42 mm of *Psidium cattleianum*

42 mm of *Psidium cattleianum*

A HONEYCOMB HEART-ROT OF OAKS CAUSED BY STEREUM SUBPILEATUM

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INTRODUCTION

During investigations made in 1912, 1913, and 1914 on the pathological condition of the oaks (*Quercus* spp.) in the National Forests of Arkansas and in other sections of the United States, the writer found a large percentage of the trees, especially in some regions of Arkansas, attacked by various species of heart-rotting fungi. Among this number were several typical delignifying fungi: *Polyporus pilotae*; *P. berkeleyi*, and *P. frondosus*, which usually occur as butt-rots;¹ and *P. dryophilus*, which produces a widely distributed top-rot in oaks.² In addition to the rots produced by these four fungi, another type of rot was found in oaks which has certain characters not assignable to any fungus known to produce heart-rot in oaks. This undescribed rot is of the pocketed type (Pl. XLI, fig. 1) and is a typical delignifier of the heartwood. In the final stage of this rot the diseased wood resembles a piece of honeycomb (Pl. XLI, fig. 2). For this reason the writer calls it the "honeycomb heart-rot." The rot is very similar to that produced by *Stereum frutulosum* in dead standing or fallen oak timber, but is distinct from it.

The writer has repeatedly found this rot directly associated with the sporophores of *S. subpileatum*. The mycelium could easily be traced from the diseased wood to the subiculum of the sporophores. The only sporophores of this fungus found were in direct association with the typical honeycomb-rot.

DESCRIPTION OF THE HONEYCOMB HEART-ROT

The pocketed or honeycomb heart-rot caused by *S. subpileatum* was found by the writer to be directly associated with the sporophores of this fungus in the following nine species of oaks: *Quercus alba*,³ *Q. lyrata*, *Q. marilandica*, *Q. michauxii*, *Q. minor*, *Q. palustris*, *Q. texana*, *Q. velutina*, and *Q. virginiana*.

¹ Long, W. H. Three undescribed heart-rots of hardwood trees, especially of oak. In Jour. Agr. Research, v. 1, no. 2, p. 109-128, pl. 7-8. 1913.

² Hedgecock, G. G., and Long, W. H. Heart-rot of oaks and poplars caused by *Polyporus dryophilus*. In Jour. Agr. Research, v. 3, no. 1, p. 65-78, pl. 8-10. 1914.

³ The nomenclature for trees used in this paper is that of George B. Sudworth. (Check list of the forest trees of the United States, their names and ranges. U. S. Dept. Agr. Div. Forestry Bul. 17, 144 p. 1898.)

HONEYCOMB HEART-ROT IN WHITE OAK

MACROSCOPIC CHARACTERS

The first indication of this honeycomb heart-rot in white oak (*Q. alba*) is a slight discoloration of the heartwood, which assumes a water-soaked appearance. This "soak" may extend from 1 to 6 feet beyond the actually rotting region where delignification is occurring. When dry, the water-soaked heartwood becomes tawny in color.

Light-colored, isolated areas appear in the discolored wood. These areas, which are the beginnings of the pockets, usually originate in the region of the large vessels and often have a small medullary ray in their centers. The rot then spreads in all directions into the surrounding tissue, but moves more rapidly in the summer wood of the annual ring of the preceding year. This results in the bulk of the pocket lying in the summer wood of one year and the spring wood of the succeeding year.

The next stage of the rot is one of delignification in which very small irregular patches of delignified wood fibers appear in the light-colored areas. This delignification, which seems to begin in the wood fibers of the preceding year's growth of summer wood immediately adjacent to a large vessel, proceeds rapidly until white, oval to circular pockets appear (Pl. XLI, fig. 3). In radial section these lens-shaped pockets range from 5 to 15 mm. long by 1 to 5 mm. wide, with their main axes parallel to the grain of the wood. These pockets are at first filled with white cellulose (Pl. XLI, fig. 3 and 4), which later is gradually absorbed, leaving cavities lined with the remnants of the cellulose (Pl. XLI, fig. 5). Sometimes long lines of cellulose fibers extend longitudinally through several adjacent cavities, but, as a rule, the cellulose is limited to each individual pocket.

The attacked area increases in size until the pockets reach a large medullary ray on either side (Pl. XLI, fig. 6). These large rays seem to check the activity of the enzymes and therefore become the boundaries of the radial walls of the pockets. They are very evident even in the badly diseased heartwood (Pl. XLI, fig. 6). This is especially noticeable in tangential and cross-sectional views. Each pocket usually does not involve more than two annual rings of growth, unless the rings are very narrow, in which case several may be included. In cross section the rot shows as irregular to circular holes from 1 to 5 mm. in diameter lying between the large medullary rays.

All the cellulose finally disappears (Pl. XLI, fig. 2 and 7), leaving the pockets either (1) empty, (2) containing the shrunken white membranes of the included vessels, or (3) more or less filled with mycelium.

In the last stage of the rot the wood is very light and of a honeycomb-like structure (Pl. XLI, fig. 2 and 7). The pockets are longer than they are broad, and all of the wood has disappeared, except the thin walls surrounding the pockets, which remain distinct and usually involve the heartwood uniformly. The rotted wood is therefore in the shape of a cylinder.

There is a brownish discoloration of the heartwood on the outer edges of the affected area. This character is also common to several other heart-rotting fungi.

When a living tree having the rot caused by *S. subpileatum* is first split open, there is a very distinct odor of old honeycomb. In some white oaks the old pockets have blackish deposits on the walls which make this rot resemble even more strongly an old, blackened honeycomb.

MICROSCOPIC CHARACTERS

A microscopic examination of the diseased wood in the initial stage of a pocket shows small groups of partially delignified wood fibers scattered in the neighborhood of the large vessels. Delignification in these wood fibers begins with the inner layer or the tertiary lamella of each fiber and proceeds outward toward the primary or middle lamella. The middle lamella is then attacked and rapidly dissolved, thus freeing each cell from its neighbor.

The walls of the small medullary rays are more slowly delignified than the wood fibers, while the walls of the large vessels resist delignification much longer than either the wood fibers or small medullary rays. The tyloses in the large vessels are the last to be delignified. They contain many small, irregular holes, apparently made by the passage of fungus hyphae through them. Delignification is not very pronounced in the cells of the radially placed rows of small vessels of the summer wood.

The pits of the vessels and the cells do not seem to be enlarged by the action of the fungus until the last stages are reached, if at all.

FUNGOUS MYCELIUM

In the earliest stages of the rot the enzymes seem to precede the fungous hyphae, especially in the region of the wood fibers. In the larger vessels a few colorless very small hyphae can be seen in the region adjacent to the area first delignified. As delignification advances, the threads in the vessels increase in number, and during the period of cellulose absorption the vessel from which the delignification started often becomes stuffed with small, intricately branched, colorless hyphae.

In the center of the pockets are often seen small, white, threadlike bodies. On examination these prove to be (1) the remnants of the delignified walls of the vessels and especially of the tyloses, which often persist even after all of the walls of the vessels have been absorbed, and (2) fungous tissue, which is composed of large (10μ), longitudinal, hyaline, thin-walled hyphae and many smaller hyphae, all interwoven into a rodlike mass.

In many of the pockets where much of the cellulose has been absorbed, dense white fluffy masses of mycelium either nearly fill or in some instances only line the cavities. This mycelium is composed of small, branched, colorless, thick-walled hyphae, some of which have granular or tuberculate walls. If the pockets border on checks or windshakes, the fluffy masses of mycelium are a reddish brown in place of white and often form a more

or less tough, brown mycelial web in the fissures of the wood. A similar mycelial growth often develops on specimens of freshly cut rotting wood from the exposed edges of the cellulose-filled cavities and may even overrun the surface of the rotting wood for several square inches.

This reddish growth seems to occur only when the actively growing hyphae are exposed to the air, since in the interior of the wood, where they are not thus exposed, the mycelium lining the original cavities caused by this fungus is white. The brownish mat of mycelium which forms in the fissures of the wood consists of dense interwoven masses of sparingly septate, fulvous hyphae. The clamp connections of these hyphae are not very pronounced, in marked contrast to those of *S. frustulosum*. These hyphae are from 2 to 3 μ thick, as a rule, but smaller ones are not uncommon with branches putting out at right angles to the main hypha. The outer walls of some of the hyphae are sparingly granular to almost tuberculate.

The very old pockets are often filled with a brownish floccose mass, which is composed of brown, tuberculate hyphae similar to those seen in the rot produced by *S. frustulosum*.

RESEMBLANCE OF THE ROT CAUSED BY STEREOUM SUBPILEATUM TO CERTAIN OTHER ROTs

It is very difficult and often impossible to separate very similar types of rot from one another, unless the fruiting bodies of the causative organism are present in direct association with the rot.

There are four delignifying heart-rots which are very similar in certain stages of their development to each other and to portions of the description given by Von Schrenk and Spaulding¹ of a piped-rot of oak and chestnut. In the light of recent investigations these four rots are now known to be caused by the following fungi: (1) *Polyporus dryophilus*, which causes a very common heart-rot in the upper portion of the trunks of oaks in the United States and is found occasionally in poplars; (2) *P. pilotae*, which attacks the heartwood of oaks and chestnuts; (3) *Stereum subpileatum*, which causes a pocketed-rot of oaks; and (4) *Hymenochaete rubiginosa*, which causes a pocketed-rot in chestnut and oak. The writer has specimens of the last-named fungus, collected during the past three years in several States and associated with a delignifying pocketed heart-rot in living chestnut. On account of the meagerness of the sporophore material, the writer was uncertain whether *H. rubiginosa* was really the cause of the rot with which it was associated or was only a secondary fungus on already diseased chestnut timber. Brown in a recent article² describes a pocketed-rot in dead chestnut and oak timber with which the sporophores of *H. rubiginosa* are constantly associated. However, he did not find it as a heart-rot in living trees.

¹Schrenk, Hermann von, and Spaulding, Perley. Diseases of deciduous forest trees. U. S. Dept. Agr. Bur. Plant Indus. Bul. 149, 85 p., 11 fig., 10 pl. 1909.

²Brown, H. P. A timber rot accompanying *Hymenochaete rubiginosa* (Schrad.) Lév. In Mycologia. v. 7, no. 1, p. 1-20, pl. 149-151. 1915.

COMPARISON OF ROTS OF STEREOUM SUBPILEATUM AND POLYPORUS PILOTAE

In the writer's investigation in the Ozarks no attempt was made in the field to separate the rot caused by *P. pilotae* from that caused by *S. subpileatum*, since both in their early stages produce small delignified areas in the diseased heartwood of living trees. It was therefore difficult to determine which fungus produced the rot unless the sporophores were present. Attention was called to this resemblance in a previous article by the writer.¹ However, the final stage of the rot produced by *P. pilotae* is quite distinct from that of *S. subpileatum*. The rot caused by *P. pilotae* usually moves upward in the infected wood, along certain well-defined zones consisting of several annual rings of growth of the wood. These zones are usually separated by zones of apparently sound tissue—that is, the rot moves upward or longitudinally in the tree more rapidly than it does radially. The rot caused by *S. subpileatum* does not seem to form definite zones of infected wood separated by sound zones, at least in the white oak, but seems to move as rapidly radially as longitudinally in the attacked heartwood, thus forming a uniform cylinder of rotted wood in the heartwood of the trees. If this character should prove constant, one could use it in field work for differentiating this rot from the earlier stages of the rot of *P. pilotae*. However, in well-advanced stages of rot, the presence of typical lens-shaped to cylindrical pockets occupying practically all of the infected heartwood is fairly indicative that the rot in question is caused by *S. subpileatum*.

ENTRANCE OF THE FUNGUS INTO THE HOST

The fungus *S. subpileatum*, so far as the writer knows, enters the wood of the hosts only through wounds which expose the heartwood. The most common point of entrance is through wounds, usually fire scars, in the butt of the trees, although it also frequently enters through branch stubs. The writer found this rot several times in the tops of living white-oak and black-oak trees in the Ozark National Forest, Arkansas. In every case the fungus had undoubtedly entered through a branch stub. It produces the same type of rot (Pl. XLI, fig. 4 and 7) in the tops as it does in the butts, even to the peculiar honeycomb-like odor.

No instances were found where this rot had entered a living tree through the dead sapwood of a wound, nor where it had entered a dead tree or log through the sapwood. It is very probable, however, that the fungus does attack dead timber in this manner, since many examples were found where the fungus had grown from the heartwood into the dead sapwood of felled trees.

¹Leag, W. H. Three undescribed heart-rots of hardwood trees, especially of oak. In Jour. Agr. Research, v. 1, no. 2, p. 109-128, pl. 7-8. 1913.

SPOROPHORE OF STEREOUM SUBPILEATUM

The sporophores of *S. subpileatum* have been found by the writer only on dead trees or on dead areas on living trees. They usually occur on the fallen trees which had this rot while living. *S. subpileatum* apparently does not attack the living sapwood and therefore has no chance to fruit unless the diseased heartwood is exposed by the death of the tree or by the breaking off of the trunk or of a branch. When an oak whose heartwood is attacked by this fungus is felled, the fungus continues to grow in the heartwood of the felled tree (Pl. XLI, fig. 8) and also grows outward into the sapwood. When the actively growing mycelium reaches the surface of the sapwood, the thin shelving sporophores (Pl. XLI, fig. 9) are formed in the cracks between the bark, or if the bark has been burned off or has fallen off, large numbers of sporophores, often conchate in shape (Pl. XLI, fig. 10), are formed over the entire surface of the fallen tree. These sporophores usually form in long, continuous parallel lines. The individual sporophores range from 0.25 to 2 inches in width, depending on their age.

Living trees with this rot when felled usually lie for two or more years before any sporophores are formed. After sporophore formation once commences, the sporophores usually continue to grow for many years; therefore a tree or log culled for this rot in a lumbering operation, if not destroyed, will after one or two years be a menace for years to the future health of the forest.

DESCRIPTION OF THE SPOROPHORE OF STEREOUM SUBPILEATUM

Pileus rather thick, medium-sized, coriaceous, firm, drying rigid and hard, sessile, dimidiate, conchate, subimbricate, often laterally connate, usually effuso-reflexed, decurrent onto the wood for 0.5 to 2 cm., 1 mm. thick by 0.5 to 6 cm. wide (measured from front to rear of sporophore) and 2 to 12 cm. or more broad, perennial, attached to substratum by a thin subiculum of densely woven Mars yellow¹ hyphae; surface finely tomentose at first, becoming glabrate with age, multizonate, older zones drab gray, finally becoming very indistinct and nearly glabrous, often radiately furrowed, marked with several concentric furrows of variable width and depth; margin thin, undulate, often incurved, strongly tomentose, tomentum from light buff to Mars yellow; hymenium inferior, sometimes stratose, changing color when injured and moistened, often concave, even, light buff; basidia simple with four sterigmata; spores colorless, even, broadly oval, flattened on one side, 4 to 5 by 3 μ ; cystidia incrustated, colorless, becoming brownish where buried in older layers of the hymenium, cylindrical, 25 to 40 by 6 to 8 μ , not present in the intermediate or tramal layer.

¹ Ridgway, Robert. Color Standards and Color Nomenclature. 43 p., 53 col. pl. Washington, D. C. 1912.

DISTRIBUTION OF *STEREUM SUBPILEATUM*

The rot caused by *S. subpileatum* is rather widely distributed in certain sections of the United States, having been found in eight States: Arkansas, Kentucky, Florida, Louisiana, Mississippi, Missouri, Ohio, and Virginia. Authentic specimens of the fungus have also been examined from Mexico. The sporophores of the fungus are frequent and the rot caused by it is common in Arkansas, Mississippi, and Louisiana.

DISTRIBUTION IN AMERICA

S. subpileatum has been reported from and collected in the various States of this country as follows:

ARKANSAS:

On *Quercus alba*.—Casteel, LONG, in August and December, 1912 (F. P. 12136,¹ 12178, 12194, 12629, 12729, 18619, 19026); Arkansas National Forest, LONG, in September, 1913 (F. P. 12703, 19016).

On *Quercus nigra*.—Arkansas City, LONG, in November, 1913 (F. P. 19065).

On *Quercus palustris*.—Arkansas City, LONG, in November, 1913 (F. P. 18405).

On *Quercus phellos*.—Arkansas City, LONG, in November, 1913 (F. P. 19064).

On *Quercus rubra*.—Lake Village, LONG, in November, 1913 (F. P. 19071).

On *Quercus texana*.—Arkansas National Forest, LONG, in September, 1913 (F. P. 18502, 18715).

On *Quercus velutina*.—Arkansas National Forest, LONG, in September, 1913 (F. P. 12567, 12724); White Rock, LONG, in September, 1912 (F. P. 12242).

FLORIDA:

On *Liquidambar styraciflua*.—(?) G. C. FISHER (No. 07643, Herb. Lloyd).

On *Quercus* sp.—C. G. LLOYD, in February, 1899 (No. 4846, Herb. Lloyd); Lake City, ROLFS and FAWCETT, in March, 1906 (Herb. Lloyd).

On *Quercus virginiana*.—New Smyrna, LONG, in March, 1914.

On *Quercus* sp. (?).—Gainesville, H. S. FAWCETT (No. 08090, Herb. Lloyd).

On wood.—G. C. FISHER (No. 07849, Herb. Lloyd).

KENTUCKY:

On *Quercus* sp. (?).—Mammoth Cave, C. G. LLOYD, in July, 1897 (No. 2798, Herb. Lloyd).

LOUISIANA:

On prostrate logs, St. Martinsville, LANGLOIS, in April, 1897 (No. 2428, Herb. Lloyd No. 5).

On *Quercus lyrata*.—Lutcher, LONG, in November, 1913 (F. P. 19067, 19091).

MISSISSIPPI:

On *Quercus phellos*.—Stoneville, LONG, in November, 1913 (F. P. 18722).

MISSOURI:

On *Quercus palustris* (?).—Steelsville, SPAULDING No. 44 (F. P. 12955).

OHIO:

On wood.—Cincinnati, A. P. MORGAN (Herb. Lloyd).

VIRGINIA:

On *Quercus alba*.—Great Falls, LONG, in 1914.

On *Quercus coccinea*.—Veitch, LONG, in 1913 (F. P. 12571).

On *Quercus prinus*.—Arlington, LONG, in 1914.

On *Quercus velutina*.—Park Lane, LONG, in 1914.

¹ "F. P." = Forest-Pathology Investigations number.

MEXICO:

On *Quercus* (?).—Jalapa, CHARLES L. SMITH, No. 146 Central American Fungi, in 1894 (No. 4709, Herb. Lloyd).

From the foregoing data it will be noted that the following trees are attacked by the disease caused by *S. subpileatum*: *Q. alba*, *Q. coccinea*, *Q. lyrata*, *Q. marilandica*, *Q. michauxii*, *Q. minor*, *Q. palustris*, *Q. phellos*, *Q. prinus*, *Q. rubra*, *Q. texana*, *Q. velutina*, *Q. virginiana*, *Quercus* spp., and *Liquidambar styraciflua* (?).

CONTROL OF THE HONEYCOMB HEART-ROT CAUSED BY *STEREUM SUBPILEATUM*

The honeycomb heart-rot caused by *S. subpileatum* is one of several important heart-rots of oaks in the United States. Suggestions made for its control will apply more or less to all of these. The fact that apparently oaks of all ages are susceptible to this rot, provided they are old enough to have formed heartwood, must be taken into consideration when discussing methods of control. The only practicable method of control known which can be applied to the forest as a whole is to prevent, so far as possible, the infection of the trees. This can be done (1) by eliminating, so far as possible, all forest fires, since they produce wounds on the butts of the trees through which the fungus enters; (2) by preventing the formation of the fruiting bodies (sporophores) of the fungus which produce the spores. These spores are the direct agents for infecting the trees through dead branches and fire scars.

The only method at present known by which the development of the sporophores of this fungus can be prevented is the destruction of all diseased timber which contains this rot. In lumbering tracts of oak all unsound or diseased trees should be cut, the parts that can be used removed, and the cull logs and dead trees burned, since this fungus fruits most abundantly on old logs and on dead fallen timber. Many trees under the present methods of lumbering are left standing because they have heart-rot in the butt. If cut down, these trees would usually be found to contain enough lumber to pay for the cost of operation. Such a procedure will lead to a better and closer utilization of our gradually decreasing supply of oak and insure a healthier future forest.

Special emphasis should be placed on the fact that the rot produced by *S. subpileatum* can continue to grow in a tree after it is felled, and that every cull butt, log, or tree left on the ground in a lumbering operation will later bear an enormous number of sporophores of this fungus which will discharge annually millions of spores for many years. In the interest of the health of the future forest, it is therefore of the utmost importance that all of these cull logs and trees be destroyed.

PLATE XLI

Fig. 1.—*Quercus alba*: A radial view of the honeycomb heart-rot produced by *Stereum subpileatum*, showing various stages of the rot; from Arkansas.

Fig. 2.—*Quercus alba*: A radial view of the last (honeycomb) stage of the rot; from Arkansas.

Fig. 3.—*Quercus alba*: A tangential view of honeycomb-rot, showing early stage of delignification; from Arkansas.

Fig. 4.—*Quercus velutina*: A radial view of honeycomb heart-rot as it occurs in tops of trees, showing pockets filled with strands of cellulose; from Arkansas.

Fig. 5.—*Quercus alba*: A radial view of the honeycomb-rot, showing pockets lined with cellulose; from Arkansas.

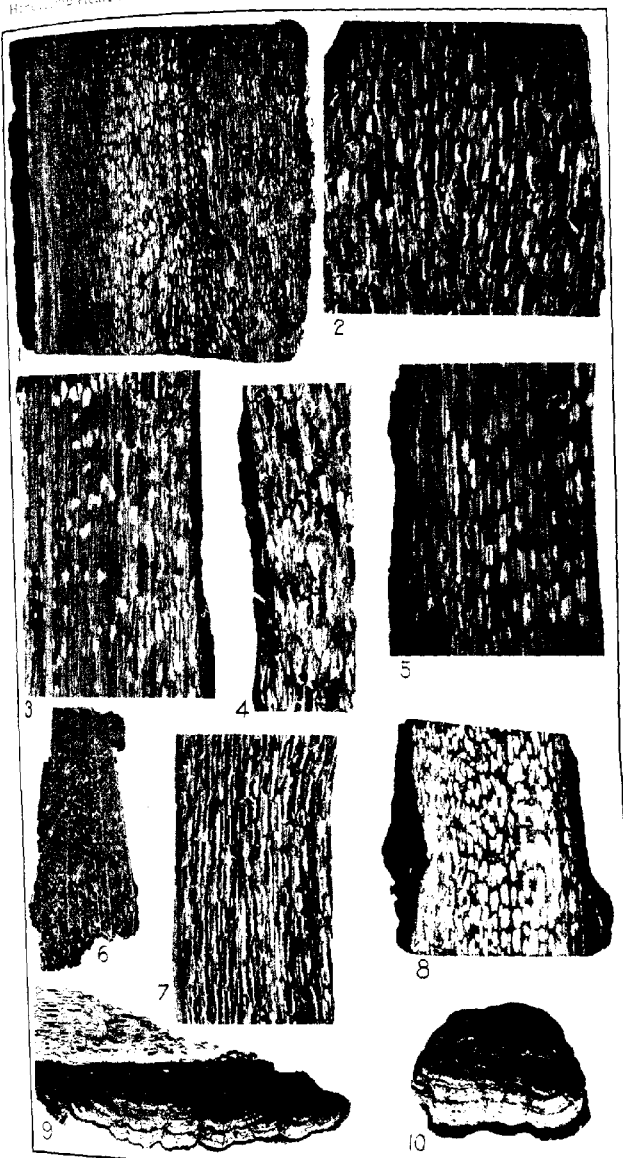
Fig. 6.—*Quercus alba*: A cross-sectional view of the honeycomb heart-rot, showing pockets limited by large medullary rays; from Arkansas.

Fig. 7.—*Quercus alba*: Radial view of honeycomb heart-rot in branch, showing last stage of rot; from Arkansas.

Fig. 8.—*Quercus lyrata*: Radial view of honeycomb heart-rot in old log associated directly with the sporophores of *S. subpileatum*; from Louisiana.

Fig. 9.—*Quercus texana*: Sporophore of *S. subpileatum*; from Arkansas.

Fig. 10.—*Quercus palustris*: Sporophore of *S. subpileatum*, conchate form; from Arkansas.



MEASUREMENT OF THE WINTER CYCLE IN THE EGG PRODUCTION OF DOMESTIC FOWL¹

By RAYMOND PEARL,

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In a series of papers the writer and his associates (2, 6, 9)² have shown that there are to be distinguished definite cycles in the egg-laying activities of the fowl. The two most striking and definite of these cycles we have called, respectively, the "winter" and the "spring" cycles, these terms being used because of the seasonal incidence of these periods of laying activity. In the writer's studies on the inheritance of fecundity (4, 5, 7, 8) in the fowl he has used as an index of the innate fecundity of a bird its pullet-year "winter production," defined as the number of eggs produced before March 1 of the bird's pullet year—i. e., the first March 1 following the individual's birth. The reasons why this measure of productivity rather than some other was chosen for the work have been fully set forth in earlier papers and need not again be gone into here. It may suffice to say that, by all the tests which it has so far been possible to apply, this index of fecundity has proved very satisfactory in practice. The results which one obtains with it are duplicated in every essential particular if one uses the longer period of one year, but genetic differences in fecundity are more strongly emphasized in the shorter period, with a corresponding gain in the precision and certainty of the Mendelian analysis.

It has never been contended, however, in any of the writer's work that winter production, as above defined, was anything more than an index or indicator of innate fecundity. It is logically obvious that the only perfect measure of total fecundity would be some direct function of total fecundity. All that the writer's work has shown regarding the point here under discussion is that winter production is a good indicator, all things considered, of a fowl's innate fecundity capacity. It is not a perfect indicator, but that it is a good one is confirmed not only by the experience of this laboratory but also by that of other workers (1, 3, 10).

In the course of the writer's investigations regarding this character, studies have been made of various other fecundity indicators besides winter production. The thought occurs to one that possibly under other environmental conditions than those prevailing in Maine winter produc-

¹ Papers from the Biological Laboratory of the Maine Agricultural Experiment Station, No. 89.

² Reference is made by number to "Literature cited," pp. 436-437.

tion might prove a less valuable and reliable indicator. This may possibly be so, though up to the present time no definite evidence on the point has appeared. Another point which occurs to one is that possibly a better measure of the winter cycle of productivity (this being the biological entity we attempt to measure by the record of production to March 1) might be obtained by using the egg production of a bird up to the time when it has attained a definite age. Fowls are hatched at different dates, while March 1 is a fixed point in time. Birds hatched at different times will be of different ages at March 1 of their pullet year. Will the egg production prior to the attainment of a definite age by a bird give a better measure of her winter cycle than the production prior to a fixed date without regard to age, except so far as this is involved in having the birds all hatched within a certain limited season? It is the purpose of this paper to present some data on this question.

Specifically the material here presented has to do with the suggestion that the egg production up to 300 days of age of the bird gives a better measure of the winter cycle than does the production to March 1, since an age of 300 days will include the winter cycle, and will also allow for differences due to variation in date of hatching. Biometrically we can readily test this question in two ways: On the one hand, we can determine the correlation between the winter production as defined by the writer (to March 1) and the production to 300 days of age, on the other hand. If this correlation is low, it will mean that one of the measures is probably sensibly better than the other. If, on the other hand, the correlation is very high, differing but little from perfect correlation, it will indicate, so far as it goes, that there is little to choose between the two measures. In the second place, we may examine the variabilities biometrically. On theoretical grounds that measure of a character is best, other things being equal, which exhibits the smallest relative variability.

Evidence along these lines derived from extensive trap-nesting experiments is presented in the following tables. The data cover three consecutive years. Two correlation tables are presented for each year: One including the total flock of that year regardless of breed distinctions, the other including only pure Barred Plymouth Rocks. The total flocks were made up of various crossbred birds used in Mendelian experiments, in addition to the pure Barred Plymouth Rocks. All birds included in the tables are pullets—i. e., they were hatched in the spring of the year indicated in the caption of the table. The computations were made by Mr. John Rice Miner, staff computer of the Biological Laboratory. See Tables I to VI.

TABLE I.—Correlation between (a) egg production to March 1, and (b) egg production to 300 days of age, for pure Barred Plymouth Rocks hatched in 1911

		EGG PRODUCTION TO 300 DAYS OF AGE.																	Total.
		0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	
EGG PRODUCTION TO MARCH 1.	0-4	8	1		1													8	
	5-9	1	2	1	1													3	
	10-14	1	1															5	
	15-19			3	6	5	1											15	
	20-24					4	5	3										14	
	25-29					7	6	5	2	1								19	
	30-34				2		7	6	4	1								16	
	35-39						4	3	3	9	3							23	
	40-44								1	3	5	1	1					10	
	45-49										4	3	1	1				12	
	50-54											4	1	1				7	
	55-59														4	1		6	
	60-64														3		1	4	
	65-69																	2	
	70-74																	2	
	75-79																	2	
80-84																	4		
85-89																	2		
90-94																	4		
95-99																	2		
100-104																	3		
Total		11	4	7	17	17	29	21	22	16	15	13	10	10	1	2	1	3	
																		199	

TABLE II.—Correlation between (a) egg production to March 1 and (b) egg production to 300 days of age, for total flock hatched in 1911

EGG PRODUCTION TO MARCH 1	EGG PRODUCTION TO 300 DAYS OF AGE.																	Total.
	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	
0-4	37																	50
5-9	13	7																34
10-14	6	8	6															31
15-19	1	5	8	5	1	1												32
20-24			9	8	2	2												39
25-29			8	17	11	11	1											38
30-34				2	11	11	1											39
35-39					1	17	13	6	2	1								39
40-44					2	10	7	3	2									26
45-49						9	5	5	5	1								32
50-54						1	9	5	5	1								35
55-59							4	4	15	7	4	1	1					38
60-64								4	19	4	1							18
65-69									1	4	1	1	1					11
70-74											3	3	4	4	2			14
75-79											2	2	4	2		1		11
80-84															2			5
85-89																1		2
90-94														1				3
95-99																		3
100-104																		3
Total	57	28	40	49	51	55	33	31	39	21	24	15	13	2	2	1	3	464

TABLE III.—Correlation between (a) egg production to March 1 and (b) egg production to 300 days of age, for pure Barred Plymouth Rocks hatched in 1912

EGG PRODUCTION TO 300 DAYS OF AGE.																		
	0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	Total.
0-4	6																	6
5-9	3	3																6
10-14	1	2	1															4
15-19		2	2	1														6
20-24	4		1	2														7
25-29		1	1	2	3	1												10
30-34		1		1	4	2	2											12
35-39			2	2	3	8	5	1			1							20
40-44				2	5	2	3	6	1									22
45-49					1	5	6	2	5									24
50-54					1	1	3	6	5	0								22
55-59							3	6	1	3	3	2						25
60-64							2	2	2	1	1							16
65-69								2	9	1	3	2						17
70-74								1	2	1	1	1						6
75-79									1	2	1	1	2					7
80-84											4	1	2	2				9
85-89													4					4
90-94															2			2
95-99																1	1	2
100-104																	1	1
105-109																		1
Total	14	8	7	10	17	19	19	20	16	22	14	9	11	4	3	4	2	196

TABLE IV.—Correlation between (a) egg production to March 1 and (b) egg production to 300 days of age, for total flock hatched in 1912

		EGG PRODUCTION TO 300 DAYS OF AGE																		Total
		0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84		
EGG PRODUCTION TO MARCH 1.	q	42	3			1													46	
	5-9	8	10																18	
	10-14	9	3	8		2	1												23	
	15-19	1	5	6	9	1													22	
	20-24		3	11	7	6	1												28	
	25-29		2	3	5	8	12	3	2	1									36	
	30-34		1		5	17	9	4	3		1								40	
	35-39			2	3	7	10	13	9	1		2							53	
	40-44				2	7	8	6	11	6		2							45	
	45-49					2	7	8	4	6	2								35	
	50-54					1	2	6	4	3	9	3							31	
	55-59						1	11	2	3	6	3							27	
	60-64							3	4	2	2	3	1						15	
	65-69								2	10	1	3	2						26	
	70-74									1	2	1	1	2					7	
	75-79									1	4	1	2	1					9	
80-84													2	3				5		
85-89																1	1	2		
90-94																		1		
95-99																		1		
100-104																		1		
105-109																		1		
Total		68	24	25	39	53	61	42	47	37	30	25	12	13	5	3	4	2	484	

TABLE V.—Correlation between (a) egg production to March 1 and (b) egg production to 300 days of age, for pure Barred Plymouth Rocks hatched in 1913

		EGG PRODUCTION TO 300 DAYS OF AGE.																							Total.
		0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100-104	105-110		
EGG PRODUCTION TO MARCH 1.	0-4	10																							11
	5-9		1																						3
	10-14			1																					1
	15-19				1																				5
	20-24					3																			9
	25-29						3																		5
	30-34							1																	7
	35-39								1																14
	40-44									1															7
	45-49										2														18
	50-54											1													18
	55-59												1												17
	60-64													1											14
	65-69														1										12
	70-74															1									22
	75-79																1								16
	80-84																	1							14
85-89																		1						21	
90-94																			1					13	
95-99																				1				6	
100-104																					1			1	
105-109																						1		6	
110-114																								1	
115-119																								1	
120-124																								1	
125-129																								1	
Total.		10	2	3	4	8	8	9	16	10	14	19	21	14	14	15	14	13	9	7	3	2	2	2	217

TABLE VI.—Correlation between (a) egg production to March 1 and (b) egg production to 300 days of age, for total flock hatched in 1913

		EGG PRODUCTION TO 300 DAYS OF AGE.																							Total.
		0-4	5-9	10-14	15-19	20-24	25-29	30-34	35-39	40-44	45-49	50-54	55-59	60-64	65-69	70-74	75-79	80-84	85-89	90-94	95-99	100-104	105-109		
EGG PRODUCTION TO MARCH 1.	0-4	37	3	2	1																				43
	5-9	12	5	2																					18
	10-14		5	3	3																				18
	15-19			2	4	10	3																		20
	20-24					3	6																		20
	25-29						7	7																	28
	30-34							8																	18
	35-39								5																29
	40-44									3															36
	45-49										1														28
	50-54											1													25
	55-59												6												22
	60-64													2											25
	65-69														1										21
	70-74															3									25
	75-79																1								21
	80-84																	1							22
	85-89																		1						25
	90-94																			1					21
	95-99																				1				25
	100-104																					1			20
	105-109																						1		3
	110-114																								7
	115-119																								1
	120-124																								1
	125-129																								1
Total.		55	20	23	18	30	26	26	25	18	31	34	33	28	24	23	20	14	14	9	3	2	2	2	478

12570°-15—3

It is evident from mere inspection of Tables I to VI that the correlation between these two variables is very high and that the regression is linear. Calculating the coefficients of correlation by the usual Bravais formula, $r = \frac{S(xy)}{N\sigma_1\sigma_2}$, with a probable error of r given by the expression

$$PE_r = \pm .67449 \frac{1-r^2}{\sqrt{n}},$$

we have the results set forth in Table VII.

TABLE VII.—Coefficients of correlation between (a) egg production to March 1 and (b) egg production to 300 days of age

Year.	Flock.	Coefficient of correlation.
1911....	Barred Plymouth Rock.....	0.955 ± 0.004
1911....	Total.....	.939 ± .004
1912....	Barred Plymouth Rock.....	.923 ± .007
1912....	Total.....	.915 ± .005
1913....	Barred Plymouth Rock.....	.940 ± .005
1913....	Total.....	.921 ± .005

These coefficients are clearly of a high order of magnitude. They fall in the same class, for example, as coefficients measuring the correlation between homologous organs on the two sides of bilaterally symmetrical organisms. These values in the present case lead unequivocally to the conclusion that with the flocks of birds here considered there certainly is no definite or marked superiority of either of these measures of the winter cycle of productivity over the other. These high correlations indicate that the two measures can be employed interchangeably so far as practical statistical work is concerned. This does not mean that the records to March 1 and to 300 days will be identical for a particular hen. What the high correlations do mean is that if an individual, A, has a higher record to March 1 than another individual, B, the probability is so high as to amount nearly to certainty that A will also have a record to 300 days which will be higher than the corresponding record of individual B and by an amount in proportion to the difference exhibited by the records to March 1.

It will be noted that the correlation for the total flock is lower than that for the Barred Plymouth Rock flock in every case. No biological significance appears to attach to these differences, which are small in amount.

The three years here dealt with are entirely typical, and an examination of our data indicates clearly that precisely the same result would be reached if we used the material from other years of the trap-nest records of the Maine Station. There was felt to be no point in piling up further correlation coefficients, all showing the same thing. The figures given above are quite sufficient to show that there is no warrant what-

ever for the assertion that the record to 300 days of age is a better measure of the winter-cycle production than is the record to March 1, so far as concerns the flocks which have been used in the writer's investigations of fecundity. Of course, it might possibly be that if one did the bulk of his hatching very late in the season, so that the pullets were not properly matured in the fall, then the 300-day record might be more reliable than the March 1 record. Tables I to VII demonstrate, however, that there is no distinct or marked superiority of one of these measures over the other when the flocks are bred and managed as those of the Maine Station have been during the last eight years.

We may turn now to an examination of the variation constants for the two measures. These are shown in Table VIII.

TABLE VIII.—*Variation constants for (a) egg production to March 1, and (b) egg production to 300 days of age*

EGGS LAID BEFORE MARCH 1				
Year.	Flock.	Mean.	Standard deviation.	Coefficient of variation.
1911....	Barred Plymouth Rock.....	43.13 ± 0.97	20.26 ± 0.69	46.98 ± 1.01
1911....	Total.....	32.45 ± .67	21.53 ± .48	67.26 ± 2.06
1912....	Barred Plymouth Rock.....	48.41 ± 1.04	21.83 ± .74	45.09 ± 1.81
1912....	Total.....	36.24 ± .68	22.09 ± .48	60.96 ± 1.75
1913....	Barred Plymouth Rock.....	59.37 ± 1.21	26.39 ± .85	44.44 ± 1.70
1913....	Total.....	47.68 ± .89	28.85 ± .63	60.51 ± 1.74
EGGS LAID BEFORE 300 DAYS OF AGE				
1911....	Barred Plymouth Rock.....	34.39 ± 0.83	17.40 ± 0.59	50.60 ± 2.10
1911....	Total.....	47.09 ± .56	17.76 ± .39	65.57 ± 1.98
1912....	Barred Plymouth Rock.....	35.97 ± .91	19.11 ± .65	53.12 ± 2.25
1912....	Total.....	28.28 ± .56	18.15 ± .39	64.16 ± 1.39
1913....	Barred Plymouth Rock.....	54.56 ± 1.12	24.38 ± .79	44.68 ± 1.71
1913....	Total.....	42.38 ± .83	26.92 ± .59	63.53 ± 1.86

From Table VIII it is apparent that, in the first place, the mean production for the 300-days-of-age group is uniformly below the mean production to March 1. Since the latter period can hardly be regarded as essentially overestimating the winter cycle, as judged on the basis of curves of the distribution of production through the year (9), clearly the 300-day grouping must somewhat underestimate in the case of flocks with a mean hatching date falling in the month of April. All the flocks which have been used in the study of fecundity at the Maine Station and on which all of our conclusions have been based have their mean date of hatching in the month of April. It is therefore plain that the 300-day measure can not in this respect be considered so good a measure of the winter cycle under the conditions prevailing in the writer's investigations as the March 1 measure.

It will be noted that the Barred Plymouth Rock means are higher throughout than are the total flock means. This merely signifies that in the total flocks are included many crossbred birds carrying low fecundity genes.

Turning to the coefficients of variation, which measure the relative variability, it is seen that in every case but one (total flock, 1911) the coefficient is lower for the March 1 than it is for the 300-day measure. The differences are, in the single instances taken by themselves, usually not statistically significant, having regard to the probable errors; but the general trend is unmistakably in the direction of a lower relative variability of the production to March 1, indicating again that this is a somewhat better measure of the winter cycle than the production to 300 days of age under the conditions prevailing in this work.

SUMMARY

In this paper quantitative evidence is presented which shows, with flocks of poultry having average hatching dates falling somewhere within the month of April, that—

(1) The correlation between the egg production to March 1 of the pullet year as one variable and the egg production up to the time when the individual is 300 days of age as the second variable is extremely high.

(2) The mean production to March 1 is, in general, higher than the mean production to 300 days of age.

(3) The production to March 1 is a relatively less variable measure (as indicated by the coefficient of variation) than the production to 300 days of age.

(4) The conclusion that the 300-day production would be a better measure of the winter cycle of fecundity than the production to March 1 is not warranted by the facts. Whatever superiority there is of one of these measures over the other is entirely in favor of the production to March 1. We may therefore conclude that the use, in the writer's investigations on fecundity, of the record of egg production to March 1 of the pullet year as a measure of the winter cycle of production is fully justified by a critical examination of the facts. The justification for the employment of the winter cycle of production as an index of innate fecundity capacity or ability is a distinct and separate problem which has been discussed at length in earlier papers.

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INFLUENCE OF GROWTH OF COWPEAS UPON SOME PHYSICAL, CHEMICAL, AND BIOLOGICAL PROPERTIES OF SOIL

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INTRODUCTION

In the past 25 years much experimental work has been done with cowpeas (*Vigna sinensis*) in relation to cultural methods, fertilization, and variety tests, but practically nothing has been written with regard to the direct effect of the plant upon the soil. Some have expressed the belief that cowpeas are capable of producing a loosening effect upon the soil, but no authentic experimental data are available.

HISTORICAL SUMMARY

An exhaustive study of research literature revealed that previous work along the particular line referred to has been exceedingly limited. The data at hand bear only indirectly upon the work of this experiment, but are worthy of consideration.

With regard to the effect of shading on soil, Bühler² reports having carried on an experiment on four broad plots of ground. One was exposed to sun and wind; the others were shaded by horizontal wooden trellises placed around each plot 40 cm. above the ground and so arranged as to cut off one-fourth, one-half, and three-fourths of the sunlight from respective screened plots.

Data at the end of the experiment showed that at midday the shaded plots had a lower temperature than the open plot by from 2 to 10 degrees centigrade. However, the cooling by night under the shaded plot was very slight, being less than 2 degrees centigrade, which explains the effectiveness of a windbreak in preventing injury by frost. In rainy weather the variation of temperature either by day or by night was much smaller.

The relative evaporation from plots throughout the test was as follows:

Treatment.	Percentage of evaporation.
No shade.....	100
One-fourth shade.....	84
One-half shade.....	71
Three-fourths shade.....	62

¹ The writer desires to acknowledge his gratitude to Prof. M. F. Miller, of the Missouri Experiment Station, under whose direction these experiments were carried out.

² Bühler, A. Influence des treillis abris sur la température du sol et sur l'évaporation. *In Ciel et Terre*, ann. 17, no. 1, p. 22-22. 1896.

Wollny¹ reports that the shade of crops on land has little or no tendency to increase the looseness of a soil, but his data show that a crop, either cereal or legume, partially prevents the land from becoming compact. He has proved that not alone is this effect due to the elimination of the effects of beating rains and sunlight thereafter but to a greatly increased bacterial activity on cropped land. The bacteria thrive better in the moderate shade afforded by the plants, produce more humus, and thus improve the soil structure. The author gives definite experimental data to substantiate his conclusions.

Stewart,² in experiments with the effect of shading on soil conditions, where tobacco under tents and in the open was grown for comparison, reports the following conclusions from his investigation. The soil under the tent remains more moist than the uncovered soil, a condition which is especially important during the dry growing period. For this reason the shaded soil is always closer to the optimum water content. Because the soil is not subject to the packing due to alternate wetting and drying, it remains in better physical condition.

PLAN OF THE WORK

The soil of the Missouri Experiment Station field, upon which this experiment was performed, analyzed as a silt loam. The surface soil to a depth of 8 inches is a grayish to brownish silt loam; from 8 to 21 inches it grades heavier and is dark red in color, and from 24 to 48 inches it becomes more granular, contains some sand, and is of a light yellowish tinge. The mechanical analysis is as follows: Fine gravel, 0.26; coarse sand, 0.37; medium sand, 10.77; fine sand, 0.77; very fine sand, 29.37; silt, 49.55; clay, 8.88; total, 99.97; volatile matter, 4.91.

This soil might be termed the Shelby silt loam, according to the classification of the United States Bureau of Soils.

Work was actively begun on the preliminary part of this investigation in 1911. The number of samples of soil to be taken from the plots for analyses in order to eliminate the errors of sampling was determined by careful trials. Again, it was necessary to experiment with a mechanical device for measuring the compactness of the soil under different treatments.

A systematic plan for sampling the plots and for making tests for compactness at periodic times was arranged so as to avoid all chance of duplication of trials on the same piece of ground.

Experimental work was necessary upon a shade device that would permit rain to pass through without much hindrance and would shut out effectively the direct rays of the sun, thus providing the desired shade effect.

¹ Wollny, Ewald. *Der Einfluss der Pflanzendecke und Beschattung* . . . p. 165. Berlin, 1877.

² Stewart, J. B. Effects of shading on soil conditions. U. S. Dept. Agr. Bur. Soils Bul. 39, 19 p., 7 fig., 4 pl. 1907.

No crop was planted on plot D, which was unplowed and kept clean (Pl. XLII, fig. 1). Plot E was also unplowed, but was planted to cowpeas (Pl. XLII, fig. 2). Plot F was plowed and planted to cowpeas (Pl. XLII, fig. 1). No crop was planted on plot G, which was plowed, artificially shaded, and kept clean (Pl. XLII, fig. 2). Plot H was also plowed and kept clean, but was without shade or cowpeas (Pl. XLII, fig. 2).

The plots were laid out on May 31, 1912. Plots F, G, and H were carefully spaded at this time. Plots D and E were scraped with a hoe to remove trash and weeds, but no further treatment was given. A week later, on June 11, plots E and F were drilled to Black cowpeas with an ordinary wheat drill, dropping the cowpeas in rows 8 inches apart at the rate of $1\frac{1}{2}$ bushels per acre. The drill was operated by pulling it at the end of a long rope so that the horses were not permitted

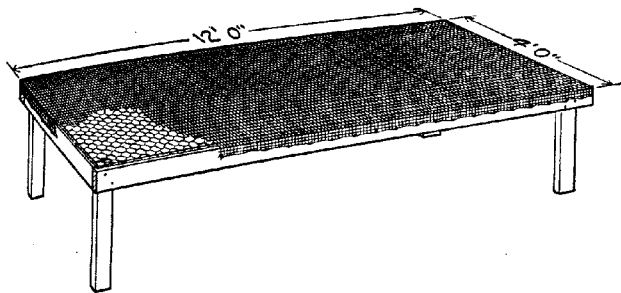


FIG. 1.—Soil-shading device, showing construction.

to walk over the plots. On June 9, after planting, all plots were gently scraped with a hoe to give them an equal start.

The main point at issue was a study of the soil compactness and nitrate content of plots in relation to the various treatments at the beginning and end of the growing season. An artificial shade was erected on plot G at a time when the cowpeas on plots E and F were matting over the soil. The shade device was a frame made of 2- by 4-inch lumber supported on legs made of the same material (fig. 1). Over this some galvanized screen was tightly stretched to serve as a support for a thin piece of black cheesecloth, which was found to be efficient in shading the soil from the direct rays of the sun and still only slightly impeding the rain.

Tests for compactness of the soil were made by counting the number of times a weighted ram had to be dropped from a specified height in order that a conical pin be driven a given distance in the soil (fig. 2). Fifteen determinations of this character were made in each plot and the average of these taken as representative.

The first observations were made on June 19, 1912. The soil was very friable at this time. Several showers had fallen since planting time, and consequently the plots were in excellent tilth.

A definite system was followed in locating places for compactness determinations, similar to the plan for taking samples for analysis. This eliminated any chance of duplicating a measurement of a given spot at later times. Tests were made at least 18 inches apart to avoid further

any influence due to overlapping. In manipulating the mechanical device (fig. 2) auger plate E was placed squarely on the ground and pin D was set in the aperture. Sheath F was then slipped over pin D, and ram G was dropped on the pin until it was driven into the soil sufficiently deep for mark *b* on the ram to be even with the top of sheath F. The ram was raised each time to mark *a* and then dropped freely by its own weight (7.445 gm.). This operation was repeated, recording each drop, until mark *c* on the ram was even with the top of sheath F. Thus, the pin was driven a distance of $4\frac{1}{2}$ inches in the ground each time a test was made. The number of drops necessary to produce this effect was the measure of the relative compactness of soil in the various plots. The results of these trials are given in Table I.

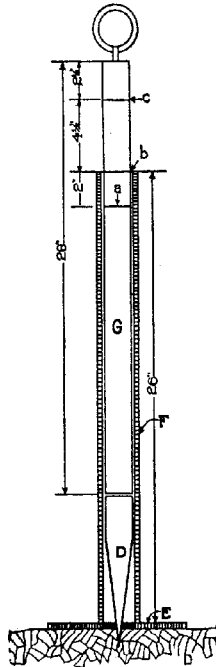


FIG. 2.—Device for testing the compactness of the soil.

The fluctuation between the readings as seen in Table I can not be accounted for other than that it represents the normal variation of soil friability over large areas. Increasing the number of readings did not materially alter the average secured. Therefore, the authentic average compactness of the plowed and that of the unplowed plots stand in the ratio of 1 to 4

at this time. Moisture determinations were made on the following day, with no rain intervening, and were as follows: All plots—first foot, 26.2 per cent; second foot, 26.5 per cent; third foot, 29.3 per cent.

On June 24 all plots were lightly cultivated with a hoe, in order to remove the weeds which had begun to appear. At this time the cowpeas were doing very well and stood about 4 inches high. Samples for nitrate analysis showed the soil to contain at the beginning of the experiment the amounts given in Table II.

As might naturally be expected, there is most nitric nitrogen in the surface foot, with a gradual decrease downward. The analysis of indi-

vidual cores also substantiates the conclusion derived from preliminary tests, that a thoroughly mixed composite is an authentic measure of the actual nitric nitrogen in the soil.

TABLE I.—*Relative compactness (number of drops of ram) of soil on the various plots at the beginning of the experiment (June 19, 1912)*

Trial No.	Plot D (unplowed; clean).	Plot E (unplowed; cowpeas).	Plot F (plowed; cowpeas).	Plot G (plowed; artificial shade).	Plot H (plowed; clean).
1.....	17	8	3	2	3
2.....	22	7	6	3	3
3.....	18	9	3	2	4
4.....	12	8	3	4	3
5.....	13	14	3	4	3
6.....	12	12	3	3	2
7.....	12	13	4	3	4
8.....	10	11	6	3	2
9.....	13	9	3	4	2
10.....	11	13	4	3	3
11.....	10	15	3	4	2
12.....	12	10	3	3	3
13.....	16	9	6	5	1
14.....	11	7	3	5	2
15.....	12	7	5	4	2
Average.....	13.3	10.5	3.6	3.4	3.6

TABLE II.—*Quantity of nitrate as NO₃ in the soil of all plots (June 24, 1912)^a*

No. of core.	Quantity of nitrate (p. p. m.)—		
	First foot.	Second foot.	Third foot.
13 C.....	6.14	3.21	5.11
14 C.....	6.93	6.13	2.37
15 C.....	6.46	3.51	3.27
16 C.....	7.26	3.20	3.66
17 C.....	12.25	3.76	3.05
18 C.....	3.93	3.25	4.78
19 C.....	9.15	4.05	2.09
20 C.....	5.86	3.69	4.35
21 C.....	7.43	3.37	2.26
22 C.....	9.30	3.76	2.58
Average.....	7.46	3.79	3.35
Composite.....	8.06	3.81	3.56
Final.....	7.76	3.80	3.45

Plate XLII shows the general plan of the experiment and the thriftiness of the cowpeas at the early date of July 17—about a month after planting the cowpeas.

^a The nitrate determinations were made by using the phenoldisulphonic-acid method, as suggested by Schriener, Oswald, and Failyer, George H., in Colorimetric, turbidity, and titration methods used in soil investigations. U. S. Dept. Agr. Bur. Soils Bul. 31, p. 39-41, 1906.

Observations taken on August 21 showed that the cowpeas on the plowed plot were only a little heavier than those on the adjacent unplowed plot. Blossoms had already begun to appear, and runners measured from 1 to 2 feet in length. Some crab-grass had sprung up, but only a few other weeds were noticed. The shade devices were in very good condition and the soil beneath seemed normal except that it was covered with a growth of green algae. This was also true of the soil of the cowpea plots, but to a less marked extent.

Great care was given to details, such as freeing from weeds, renewing the covering of the shade device, etc., throughout the season. Just before frost, compactness tests were again made on all plots after removing the cowpea vines. The vines were cut with a scythe and the strip walked on by the operator was eliminated from the test areas. The data on soil compactness secured for October 15 are given in Table III.

TABLE III.—Relative compactness (number of drops of ram) of soil on the various plots, as measured on October 15, 1912

Trial No.	Plot D (unplowed; clean).	Plot E (unplowed; cowpeas).	Plot F (plowed; cowpeas).	Plot G (plowed; arti- ficial shade).	Plot H (plowed; clean).
1	20	18	4	6	5
2	19	12	5	6	6
3	17	19	3	5	7
4	18	11	3	6	6
5	20	14	5	6	6
6	24	17	3	6	5
7	20	14	4	6	5
8	20	15	3	5	5
9	19	17	3	5	7
10	22	17	5	5	6
11	16	15	4	7	8
12	16	15	5	6	5
13	23	15	3	6	5
14	19	3	4	7	6
15	19	18	5	7	5
16	20	16	3	6	7
17	21	16	4	6	7
18	18	15	5	6	8
19	19	11	5	5	6
Average	19.4	15.4	4	5.9	6

The relative compactness as shown in Table III was duplicated, using a modification of the method which originated with Wollny¹—i. e., the apparent specific gravity of the soil in each plot was determined. A metallic brass tube 7.8 cm. in diameter was driven to a depth of 23.2 cm. in the soil. The tube was then dug out and the contact below broken. Duplicate cores of soil from each plot were thus secured, taken to the laboratory, dried, and weighed. The dry weight of the soil divided by the volume of the cylinder (1.465 c. c.) is the apparent specific gravity

¹Wollny, Ewald. Der Einfluss der Pflanzendecke und Beschattung . . . 197 p., 10 pl. Berlin, 1896.

and should be an index to friability (Table IV). Wollny compared the porosity of cores similarly taken by measuring the relative amounts of water needed to fill the pore space, but the principle is the same in both cases.

TABLE IV.—*Apparent specific gravity of soil under various treatments as determined on October 15, 1912*

Plot No. and treatment.	Weight of soil.		Average weight of core.	Apparent specific gravity.
	Core No. 1.	Core No. 2.		
	Gm.	Gm.	Gm.	
D (unplowed; clean).....	1,957	1,936	1,946	1.33
E (unplowed; cowpeas).....	1,865	1,884	1,884	1.26
F (plowed; cowpeas).....	1,720	1,739	1,729	1.17
F (plowed; shade).....	1,740	1,752	1,746	1.18
G (plowed; clean).....	1,635	1,742	1,756	1.19

Checking the results found by the Wollny method with those shown in Table III, the same ratio is found to hold in every case. This gives strong assurance that the use of the compactness device, by means of which the results of Table III were obtained, is an accurate method of measuring soil friability, and, in that it is easily and rapidly made, a very desirable one.

TABLE V.—*Percentage of moisture in the various experimental plots on October 15, 1912*

Plot No. and treatment.	Percentage of moisture.			
	First foot.	Second foot.	Third foot.	Fourth foot.
D (unplowed; clean).....	17.9	29.4	24.2	22.5
E (unplowed; cowpeas).....	25.2	28.1	17.9	13.0
F (plowed; cowpeas).....	21.7	26.1	16.5	18.8
G (plowed; shade).....	19.2	29.0	25.9	26.9
H (plowed; clean).....	11.2	28.3	27.9	25.3

A study of the moisture in the soil at the close of the experiment, as shown by Table V, reveals, as would be expected, that the plots in cowpeas leave less moisture in the soil than do the uncropped plots kept clean. However, this use of water is from below the second foot. Under cowpeas the surface foot, as well as the second foot, contains as much water as is found in the uncropped plots for the same depth. It would seem, then, that the cowpea plant is a comparatively deep feeder and the shade of its leaves serves as a blanket to prevent evaporation. This conclusion is again borne out by a study of the moisture content of the soil under the artificial shade.

Now, since only the moisture in the first foot could possibly affect the degree of compactness or of looseness at any one time, a direct comparison

of the data given in Table III with those secured at the beginning of the experiment (Table I) can be made, for on October 15 the moisture in the first foot of every plot except H was within the limit of variation, where by preliminary tests the effects due to water can be appreciated by our means of measurement. Therefore, disregarding water as a factor, it is apparent that cowpeas possibly have a tendency to maintain the friability of either plowed or unplowed land. The data also show that the plot G, plowed and artificially shaded, was almost as compact as the adjoining plowed plot (H) which was not shaded. This may be interpreted either that the shade was inefficient or that the loosening of the soil is due to some other factor. From the conclusions of Wollny¹ on this point and from the experimental data to be presented below it seems probable that this preservation of soil structure is due to increased bacterial activity, resulting in the formation of humus. This was actually demonstrated by Wollny.

The nitrate analysis of the plots at the close of the experiment, together with the bacterial count and the nitrifying and ammonifying efficiency, is given in Table VI.

TABLE VI.—Nitrate analysis, bacterial count, and nitrifying and ammonifying efficiency of soil on October 15, 1912

Item.	Depth.	Plot D (unplowed; clean).	Plot E (unplowed; cowpeas).	Plot F (plowed; cowpeas).	Plot G (plowed; shaded).	Plot H (plowed; clean).
Nitrate as NO ₃ ... p. p. m. .	First foot...	16.93	9.76	17.833	5.06	10.91
	Second foot	5.88	4.42	7.08	11.55	10.30
	Third foot..	6.31	9.18	4.08	18.42	10.30
	Fourth foot	4.42	3.73	4.48	4.72	7.66
Number of bacteria per gram of soil.	First foot..	8,481,000	29,985,000	17,929,000	9,344,400	7,729,000
Ammonifying efficiency. ^ado.....	197.19	166.20	177.50	163.80	167.20
Nitrifying efficiency.do.....	73.50	65.40	99.25	124.25	-5.50

^a The determination of ammonia in the ammonifying-efficiency studies was made by the distillation and titration method.

The amounts of nitric nitrogen in the soil in the fall, as shown by the data of Table VI, reveal the fact that all plots are going into winter with more available nitrogen in the soil than they contained in the early spring, as shown in Table II. It is also seen that cultivated plots, either cropped or uncropped, are richer in nitric nitrogen at the end of the season than are the plots not plowed. The low nitrate content of the first foot of the plot artificially shaded can not be explained. Lastly, the results check with previous investigations in the fact that under even a legume treatment there exists less nitrate in the soil in the fall than

¹ Wollny, Ewald. Op. cit.

under adjacent, similarly treated, fallowed plots. (See "Historical summary.")

Although there is a wide range in the total bacterial count under the respective treatments, the only certain conclusion which can be drawn is that under cowpeas we have larger numbers of bacteria than where no crop is on the land. The ammonifying and nitrifying efficiency of these soils as affected by the summer's treatment seemed to have been only influenced by the varied conditions noted, but no correlations can be drawn. Thus, briefly summing up, it might be said that the maintenance of soil structure from spring to fall by the growth of cowpeas on the land is due partially to the shading effect of the foliage, which, like the artificial shade, resists the compacting effect of beating rains and baking sun. Besides this, there seems to be a marked correlation between the friability of the soil under cowpeas and the bacterial flora present. Where present in largest numbers, they possibly bring about a greater production of active humus and so maintain the looseness of the soil.

SUMMARY

(1) The data given show conclusively that cowpeas tend to maintain the friability of loose and compact seed beds.

(2) It was also noted that, while cowpeas take more water from the soil than evaporates from uncultivated adjacent lands, the removal of water is from below the second foot of soil.

(3) Land that was plowed and left uncultivated or plowed and seeded to cowpeas contained a greater quantity of nitrates in the soil at the end of the season than unplowed land similarly treated.

(4) The bacterial activities of the soil upon which cowpeas were grown tended to show that the soil organisms are probably a factor in preventing the packing of soil, as also is the mechanical shade effect of the crop grown upon the land.

PLATE XLII

Experimental plots at Missouri Experiment Station:

Fig. 1.—Plot D (right), unplowed, no crop, kept clean; plot E (center), unplowed, planted to cowpeas; plot F (left), plowed, planted to cowpeas.

Fig. 2.—Plot G (right), plowed, no crop, artificially shaded; plot H (left), plowed, no crop, kept clean.

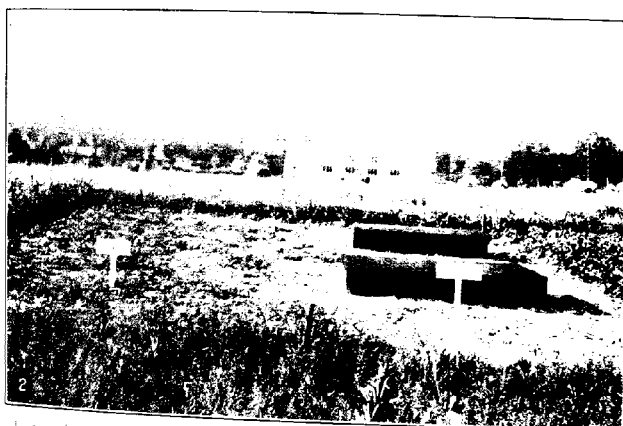
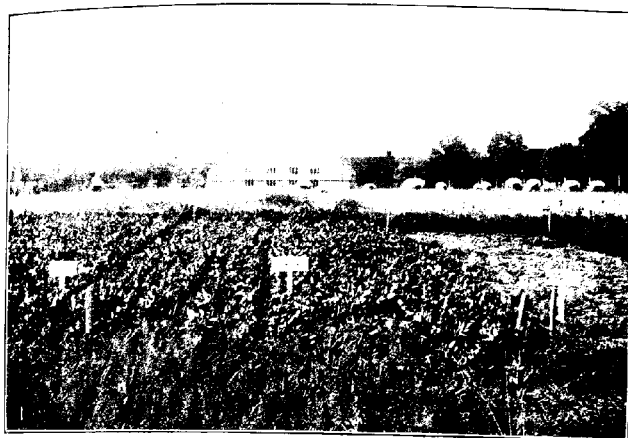


Figure 1 A standard Reservoir